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PREDICTORS OF VIGILANCE FOR AMERICAN CROWS FORAGING IN AN URBAN ENVIRONMENT

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ABSTRACT.—We examined ways in which American Crows (*Corvus brachyrhynchos*) foraging in an urban environment balance the conflicting demands of finding food and avoiding predators. As individual vigilance (i.e., scanning) decreased, time devoted to foraging increased. Significant predictors of vigilance varied with location and included time of day, temperature, food availability, distance to nearest source of disturbance, cover distance, and size of foraging group. Group size and, secondarily, distance from cover accounted for most of the variability in vigilance. Crows were more vigilant in areas of high human disturbance than in areas of low human disturbance. *Received 21 June 1996, accepted 10 Feb. 1997.*

Vigilance (used interchangeably with scanning) and foraging are mutually exclusive behaviors—a bird cannot simultaneously scan its environment for predators while feeding. Those individuals that successfully balance the tradeoffs among various costly but beneficial behaviors will yield the greatest net benefits in terms of enhanced survivorship, reproduction, and, ultimately, increased levels of fitness (Krebs and Kacelnik 1991). Here we examined the conditions under which American Crows (*Corvus brachyrhynchos*) foraging in an urban environment are able to minimize the time spent vigilant and, thereby, maximize the time available for feeding.

Individual vigilance has most often been shown to decrease with increasing group size (Bertram 1980, Heathrote 1987, Petit and Bildstein 1987) because more eyes are thought to be available for predator detection (Pulliam 1973). Several authors have shown that vigilance is also affected by proximity to danger (Elgar 1986, Westcott and Cockburn 1988), visual obstructions in the environment (Underwood 1982, Metcalfe 1984), temperature (Beveridge and Deag 1987), food availability (Barnard 1980), time of day (Pöysä 1991), and distance to cover (Barnard 1980, Carey 1985). The objectives of this study were to determine if group size, cover distance, time of day, ambient temperature, distance to nearest disturbance, and precipitation levels were predictors of crow vigilance in urban areas with different levels of human disturbance and cover. Additionally, we examined whether vigilance varied with level of human disturbance.

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STUDY AREA AND METHODS

We observed crows between May 1993 and August 1993 in Ann Arbor, Michigan (42°18'N, 83°43'W), an urban college town (population 110,000) comprised of housing developments, business districts, woodlots, and open fields. In a manner established by random design (Remington and Schork 1985), data were recorded for crows foraging on green sites throughout the city. When a solitary individual or group was spotted, we waited a minimum of 5 min or until the bird(s) stopped consistent scanning in my direction before recording observations from my car, which functioned as a blind. Single crows were selected randomly from groups (Altmann 1974) without preference given to location within a group relative to other members, distance to blind or other observers, or any other correlates that could systematically bias the data. All behaviors and their duration were recorded over a 5-min. observation period. An observation period was halted if the focal bird moved out of sight, and observations less than 3 min. in length were discarded. Observation periods averaged 4.8 min. in length. Birds were watched during the breeding season, but all data pertain to adult birds. Only one bird was sampled per group, and no location was visited more than once.

Environmental variables measured included cover distance, cover type, group size, distance to nearest disturbance, level of human disturbance, time of day, level of current and previous day's precipitation, and ambient temperature. Distances to cover and nearest disturbance were initially estimated for each focal bird and, where possible, verified by pacing. Estimates were paced in 78% of the samples collected. Birds were considered part of a group if they were observed foraging together. All observations were made on small groups (one to seven individuals), with a mean distance of less than 10 m between individuals. Group members normally arrived together to feed and departed as a group. Vigilant behavior was classified as an interruption in foraging to scan the environment, and foraging behavior was classified as a peck or probe (see Remsen and Robinson 1990 for classification of feeding behaviors). Disturbance was any potential source of danger such as an observer (Elgar 1986, Glück 1987), perceived predator (Pöysä 1989), or noise. We classified level of human disturbance based partly on Mathisen (1968), taking into consideration both the extent of structural development and human activity within the vicinity of the foraging site (Table 1).

Precipitation was used as an estimate of food availability because rain induces earthworms (pers. obs.) and ground-dwelling insects to move up near the earth's surface (Villani and Wright 1988, 1990), making prey more accessible to a foraging bird. Data were collected on crows foraging on lawns or in fields for insects, a major portion of their diet during the warmer months (Good 1952). Precipitation was classified as none, light, moderate, or heavy based on duration prior to recording behavior. Light rain lasted up to one hour, moderate rain up to three hours, and heavy rain more than three hours on any given day.

Cover type was recorded as either protective or obstructive (Lazarus and Symonds 1992). Obstructive cover was opaque and minimized visibility across all planes, for example, a solid hedgerow, forest edge, or tight group of trees. Protective cover allowed maximum visibility overhead and on a horizontal plane with the foraging crow. Examples included a single tree or an open scattering of trees. Crows frequently were observed flying into protective cover. A single tree or group of trees loosely spaced should offer protection in the event of attack by a predator, but a tight cluster of trees obstructs visibility and may actually harbor a predator hidden from view (Lazarus and Symonds 1992). Observations were made on crows foraging near either protective or obstructive cover but not near both.

The independent variables group size, cover distance, time of day, ambient temperature, distance to nearest disturbance, and duration of current day's and previous day's precipitation

TABLE 1
LEVEL OF HUMAN DISTURBANCE WITHIN 0.20 TO 0.40 KM RADIUS OF A FORAGING SITE FOR AMERICAN CROWS[a]

High	Low
Built structures and roads congesting site (e.g., suburban neighborhood, downtown business district)	Built structures and roads few and scattered (e.g., agricultural setting on the edge of town)
Birds foraging in a small, isolated patch (e.g., island of grass in a parking lot)	Birds foraging in a medium/large open area (e.g., golf course, ball field)
Ratio of green space to the built environment ≤ 1:1	Ratio of green space to the built environment > 1:1
Moderate to high levels of human activity, including pedestrian traffic and human voices	Low level of human activity; one or two pedestrian sightings
Constant vehicular traffic coming from two or more sides of site	Infrequent vehicular traffic coming from no more than one side of site

[a] All five criteria in either category were given equal weight. A site had to have met three of the five criteria in either category for classification.

were measured against the dependent variable percent time vigilant for each focal bird. Because cover type and level of human disturbance did not interact to affect vigilance (two-way ANOVA, $F = 0.89$, N = 46, $P = 0.349$, square root of percent time vigilant), we examined the relationship between vigilance and the independent variables separately by level of human disturbance (N = 23 each for high and low) and cover type (N = 26 for protective, N = 20 for obstructive). Vigilance was also examined using all data pooled (N = 45, time of day not measured for one observation period) without respect to level of human disturbance or cover type. Sample sizes corresponded to the number of 5-min. observation periods recorded for analysis.

We used stepwise regression procedures (Draper and Smith 1981, Neter et al. 1990) with alpha (α) to enter and remove each variable set at 0.10 to minimize multicollinearity in the final model. Only significant variables were included in the final model. Square root transformations of the dependent variable were used to stabilize variances for regression analyses except with data from high disturbance areas, where no transformation was necessary. Regression variables were examined individually using Pearson's correlation tests (r). Except as noted, α was set at 0.05.

RESULTS

Vigilance decreased as group size, time of day, distance to disturbance, and duration of the current day's precipitation increased ($F = 14.52$, $P < 0.0005$) for crows foraging in an urban environment. The independent variables explained 59.2% of the total variability in vigilance, with group size the strongest predictor (Table 2). When the variables were examined individually, only group size was correlated with vigilance ($r = -0.60$, $P < 0.0005$, for groups containing one to seven birds). Crows that scanned less devoted more time to feeding ($r = -0.86$, $P < 0.0005$).

TABLE 2

RESULTS OF STEPWISE REGRESSION MODEL FOR OVERALL PREDICTORS OF VIGILANCE IN AN URBAN ENVIRONMENT

Independent variables[a]	Coefficient ± SE[b]	r^{2c}	P^{b}
Group size	−0.581 ± 0.090	36.3	<0.0005
Time of day	−0.003 ± 0.001	11.4	0.001
Distance to disturbance	−0.010 ± 0.004	6.9	0.016
Current precipitation	−0.382 ± 0.180	4.6	0.039

[a] Square root of percent time vigilant as dependent variable.
[b] Coeffecients and *P*-values from final model.
[c] Percent increase in r^2 with the addition of each independent variable.

In areas of high human disturbance, vigilance decreased as group size, duration of the previous day's precipitation, and current day's precipitation increased and distance from cover decreased ($F = 28.45$, $P < 0.0005$). Cover distance included both protective and obstructive cover combined, but the number of observations near protective cover was higher than the number near obstructive cover at $\alpha = 0.10$ ($\chi^2 = 3.52$, $N_1 = 16$, $N_2 = 7$, $P < 0.10$). Therefore, the positive correlation between cover distance and vigilance may actually reflect the relationship between vigilance and distance from protective cover. The independent variables explained 86.3% of the total variability in vigilance, with group size the strongest predictor (Table 3). When the variables were examined individually, only group size was correlated with vigilance ($r = -0.73$, $P = 0.001$, for groups containing one to seven birds).

Crows were also more vigilant in areas of high human disturbance than in areas of low human disturbance (ANOVA, $F = 14.78$, $P < 0.0005$, square root of percent time vigilant). Percent time vigilant averaged 21.2% in high disturbance areas and 9.5% in low disturbance areas. This

TABLE 3

RESULTS OF STEPWISE REGRESSION MODEL FOR HIGH DISTURBANCE AREAS

Independent variables[a]	Coefficient ± SE[b]	r^{2c}	P^{b}
Group size	−4.952 ± 0.666	54.0	<0.0005
Previous precipitation	−5.749 ± 1.148	12.6	<0.0005
Cover distance	0.228 ± 0.069	12.9	0.004
Current precipitation	−3.300 ± 1.101	6.8	0.008

[a] Percent time vigilant as dependent variable.
[b] Coefficients and *P*-values from final model.
[c] Percent increase in r^2 with the addition of each independent variable.

TABLE 4

RESULTS OF STEPWISE REGRESSION MODEL FOR LOW DISTURBANCE AREAS

Independent variables[a]	Coefficient ± SE[b]	r^{2c}	P^b
Distance to disturbance	−0.009 ± 0.003	20.3	0.014
Temperature	−0.049 ± 0.019	13.8	0.020
Group size	−0.209 ± 0.094	13.6	0.038

[a] Square root of percent time vigilant as dependent variable.
[b] Coefficients and *P*-values from final model.
[c] Percent increase in r^2 with the addition of each independent variable.

result was independent of group size, as we found no difference in mean group size between high and low disturbance areas (ANOVA, $F = 1.20$, $P = 0.27$). Group size averaged 2.6 birds in high disturbance areas and 3.1 birds in low disturbance areas.

In areas of low human disturbance, vigilance decreased as distance to disturbance, temperature, and group size increased ($F = 4.52$, $P = 0.006$). The independent variables explained 47.7% of the total variability in vigilance with distance to disturbance the strongest predictor (Table 4). Individually, none of the variables was correlated with vigilance.

When protective and obstructive cover types were combined and the overall effects analyzed, we found no correlation between cover distance and vigilance ($r = -0.03$, $P = 0.81$). When broken down, cover distance was correlated with vigilance both near protective and obstructive cover. Near obstructive cover, vigilance decreased as group size and distance to nearest disturbance increased ($F = 11.62$, $P = 0.001$). The independent variables explained 57.8% of the total variability in vigilance, with group size the strongest predictor (Table 5). Individually, only group size was correlated with vigilance ($r = -0.68$, $P = 0.001$, for groups containing one to five birds). Because of the multicollinearity between group size and cover distance ($r = 0.69$), cover distance was not incorporated in the

TABLE 5

RESULTS OF STEPWISE REGRESSION MODEL FOR AREAS NEAR OBSTRUCTIVE COVER

Independent variables[a]	Coefficient ± SE[b]	r^{2c}	P^b
Group size	−0.648 ± 0.177	46.5	0.002
Distance to disturbance	−0.011 ± 0.005	11.3	0.048

[a] Square root of percent time vigilant as dependent variable.
[b] Coefficients and *P*-values from final model.
[c] Percent increase in r^2 with the addition of each independent variable.

TABLE 6

RESULTS OF STEPWISE REGRESSION MODEL FOR AREAS NEAR PROTECTIVE COVER

Independent variables[a]	Coefficient ± SE[b]	r^{2c}	P^{b}
Cover distance	0.048 ± 0.009	37.9	<0.0005
Group size	−0.395 ± 0.080	28.5	<0.0005
Temperature	0.073 ± 0.027	8.2	0.014

[a] Square root of percent time vigilant as dependent variable.
[b] Coefficients and P-values from final model.
[c] Percent increase in r^2 with the addition of each independent variable.

multiple regression model. Examined individually, cover distance explained 20.7% of the variability in vigilance ($F = 4.70$, $P = 0.044$).

Near protective cover, vigilance decreased as cover distance and temperature decreased and group size increased ($F = 21.53$, $P < 0.0005$). The independent variables explained 74.6% of the total variability in vigilance with cover distance the strongest predictor (Table 6). Individually, only cover distance (r = 0.61, $P = 0.008$) and group size ($r = -0.58$, $P = 0.015$, for groups containing one to seven birds), were correlated with vigilance.

DISCUSSION

Group size, beyond all other variables measured, was the most effective predictor of vigilant behavior in foraging crows. Its prime importance in high disturbance areas may reflect an individual's assessment of its own vulnerability. Visual obstructions and increased structural complexity, characteristics of high disturbance areas, reduce the distance from which birds can visually detect predators. Escape from a predator may be less likely if a predator is able to initiate an attack closer to its prey (Metcalfe 1984). Group formation among crows foraging in high disturbance areas probably works as a form of vigilance sharing among group members. Such sharing may be especially important in high disturbance areas, where increased rates of vigilance leave less time available for feeding.

Group formation in low disturbance areas was less important than group formation in high disturbance areas as a predictor of individual vigilance. Because structural complexity and human activity is minimized in low disturbance areas, predation pressure may not be as effective a predictor of group size and vigilance; although even in areas of low human disturbance, the threat of predation is never completely removed. The similarity in group sizes between high and low disturbance areas, suggests that crows probably group together for reasons other than strictly predator detection. Kin selection, reproduction, social learning, and possibly enhancement of food acquisition all may be associated with group formation in American Crows (Kilham 1989).

Group size was a more effective predictor of vigilance near obstructive cover than near protective cover. Because good or abundant urban foraging sites may, in fact, be located near obstructive cover, group foraging might be one strategy crows employ to increase the number of foraging sites available to them without a significant increase in risk of predation. Also, because crows frequently forage within and defend a nesting territory (Kilham 1989), group formation may be one way to overcome the potential negative consequences of a territory surrounded primarily by obstructive cover. The negative correlation between cover distance and vigilance, although marginally significant, suggests that group foraging can never completely eliminate the risk of attack initiated from behind obstructive cover.

Cover distance was a more effective predictor of vigilance than group size near protective cover. Protective cover, which is minimally obstructive and less likely to harbor an undetected predator than obstructive cover, may offer a safe retreat to a crow fleeing danger. Therefore, group foraging may not be as important near protective cover as it would be near obstructive cover, especially if the birds perceive less danger or risk of attack near protective cover. My results agree with the findings of Lazarus and Symonds (1992) who found similar relationships between vigilance and distance from protective and obstructive cover types for both House Sparrows (*Passer domesticus*) and European Starlings (*Sturnus vulgaris*).

Predator activity and frequency are normally greatest early in the morning (Pöysä 1989, 1991) and at night (Kilham 1989), which may account for the increased vigilance early in the day with pooled data. The indirect correlation between precipitation and vigilance indicate that crows may spend less time being vigilant when food is readily available in areas of high human disturbance. Barnard (1980) found similar results with House Sparrows which decreased scanning as seed density increased.

Distance to nearest disturbance may have been the strongest predictor of vigilance in areas of low human disturbance, because in areas with little noise, human traffic, and high visibility, crows may have been especially sensitive to an occasional noise or disturbance when it did occur. Such findings support those of Westcott and Cockburn (1988) who found that both Red-rumped Parrots (*Psephotus haematonotus*) and Galahs (*Cacatua roseicapilla*) increased scanning rates near noise, and Elgar (1986) found that House Sparrows increased scanning as proximity to human observers decreased. In high disturbance areas, with persistent noise and activity, sensitivity to individual disturbances would be difficult.

Temperature was a conflicting predictor of vigilance in areas of low human disturbance and near protective cover. Beveridge and Deag (1987) found that House Sparrows and Starlings scan more at warmer temperatures because the birds are looking for potential mates or rivals associated with reproduction; and Chaffinches (*Fringilla coelebs*) scan more at lower temperatures because the birds are watching for conspecifics who may have located a more profitable food source. The current literature on temperature and vigilance is often contradictory and does not take into account the effects of locational differences. For crows, the importance of temperature is apparent only in the context of the surrounding environment.

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